

Effects of Riparian and Grassland Habitats on Ground Beetle (Coleoptera: Carabidae) Assemblages in Adjacent Wheat Fields

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ABSTRACT Natural habitats surrounding agricultural fields provide a source of natural enemies to assist in pest control. The boundaries among landscape elements filter some organisms attempting to cross them, resulting in differing communities within the landscape elements. Ground beetles are numerous and generally disperse by walking. These qualities make them excellent organisms for the study of boundary dynamics. Our goal was to determine if natural habitats adjacent to wheat fields affected the species composition of ground beetles within the wheat fields. We captured ground beetles from autumn through spring 1996–1997 at two sites using directional pitfall traps placed in wheat fields and adjacent grasslands and riparian zones. Ground beetle abundance reached two peaks, one in autumn and the other in spring. Species composition was most strongly related to these seasons. Axis 1 of a canonical correspondence analysis separated spring active beetles from autumn active beetles. Axis 2 separated winter active beetles. With the effects of season and sites removed, axes 1 and 2 of a partial canonical correspondence analysis separated beetles with respect to habitat. Axis 1 separated beetles into wheat and natural habitat assemblages. Axis 2 further distinguished assemblages in wheat fields as those adjacent to grasslands and those adjacent to riparian habitats. Axis 2 also separated grassland, grassland edge, and riparian edge assemblages from riparian assemblages. Net dispersal of beetles across the boundaries showed no consistent pattern during autumn, winter, or spring. However, mark-recapture studies showed that several species routinely cross boundaries, which resulted in different community structures and an increase in abundance of beetles in the wheat interiors during spring.

KEY WORDS *Triticum aestivum*, predators, multivariate analysis, boundaries, agroecosystems, dispersal

AGRICULTURAL LANDSCAPES ARE fragmented into a mosaic of natural and anthropogenic land uses. In north-central Oklahoma, this mosaic is a patchwork primarily of grasslands, riparian zones, and croplands. Grasslands and riparian zones serve many ecological functions for plants and animals, including permanent habitats, dispersal corridors, and overwintering sites (Spence 1979; Forman and Godron 1981, 1986; Malanson 1993). Many species that overwinter in grasslands and riparian zones are beneficial to agricultural systems (Spence 1979; Sotherton 1984, 1985). These species disperse from natural habitats and colonize adjacent and nearby fields. Ground beetles are important predators of agricultural pests and many disperse only by walking (Thiele 1977, Allen 1979, Luff 1987, Lövei and Sunderland 1996). Dispersal of ground beetles among patches in an agricultural landscape connects local populations (Duelli et al. 1990). However, connectivity of the landscape to local populations of ground beetles differs among species due to the spatial configuration of landscape elements and the filtering effect of

boundaries (Wiens et al. 1985, Mauremooto et al. 1995, Pickett and Cadenasso 1995, Wiens 1997). This filtering greatly affects the colonization of ephemeral habitats such as wheat fields (Wiens et al. 1985, Mauremooto et al. 1995, Wiens 1997, Wissinger 1997).

Wissinger (1997) suggested that natural enemies inhabiting ephemeral crops such as wheat fields colonize the crops under favorable conditions and retreat to surrounding natural habitats under adverse conditions. This results in a cyclic colonization process, where natural habitats adjacent to, or near, ephemeral habitats serve as refugia. In northern latitudes where spring wheat is grown, many ground beetle species overwinter in grassy and wooded habitats surrounding wheat fields and disperse into the fields during spring (Wallin 1985, Coombes and Sotherton 1986). Seasonal patterns of use of wheat fields by ground beetles have not been studied in southern latitudes where winter wheat is grown. However, it seems reasonable to expect that ground beetles colonize winter wheat fields in autumn, emigrate to natural habitats as winter approaches, and in spring move back into the winter wheat fields. We previously described the spatial and temporal distribution of ground beetle assemblages in winter wheat fields, grasslands, and riparian zones (French and Elliott 1999a, 1999b). We found distinct autumn, winter, and spring beetle assemblages in

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wheat, grassland, and riparian habitats. Furthermore, we found that grassland, wheat, and riparian communities differed in species composition and relative abundances. Riparian communities have many distinct species, whereas grassland and wheat communities share most species. However, we did not explore whether the wheat assemblages originated from the grasslands or riparian habitats. In addition, because they were separate studies, we could not differentiate temporal variation in beetle assemblages from that due to variation in the habitats. Here we investigated the spatial and temporal structure of ground beetle assemblages in winter wheat fields adjacent to grasslands and riparian zones. We attempted to answer the following questions. Do ground beetle assemblages differ among wheat fields, grasslands, and riparian zones? Do those in adjacent habitats affect ground beetle assemblages in wheat fields? To help answer this second question we attempted to measure the dispersal of ground beetles across the boundaries of grasslands and riparian zones with wheat fields.

Materials and Methods

We established two study sites in the autumn of 1996 in fields of winter wheat (*Triticum aestivum* L.) and adjacent grass pastures (numbers 1g and 2g) and riparian zones (numbers 1r and 2r) in Noble County, OK. These study sites were separated by ≈ 10 km. The grass pastures and riparian zones abutted the same wheat fields on different sides. These sites are located in northcentral Oklahoma and are within the tall grass prairie region of the southern Great Plains (Kaul 1986). The size of the grassland at site 1 was 8 ha and at site 2 was 16 ha. The size of the wheat field at site 1 was 18 ha and at site 2 was 40 ha. The riparian zones, ≈ 30 m wide, were situated along unnamed creeks.

Sampling with Pitfall Traps. We captured ground beetles in grasslands and riparian zones adjacent to wheat fields using pitfall traps. Trap design was similar to that used by Morrill et al. (1990). In constructing the traps, we used Nalgene (Nalge, Rochester, NY) polypropylene funnels (14.5 cm i.d.) with 125-ml Nalgene plastic containers attached beneath to confine the ground beetles. To provide for easy exchange of containers, we glued the screw top caps of the plastic containers to the base of the funnels. We cut out the bottoms of the containers and replaced them with screen mesh (12.6 strands per centimeter) to permit water to pass through the container while retaining the ground beetles. We then placed 1.5 by 1.5-cm pieces of Ectrin (Fermenta Animal Health, Kansas City, KS) insecticide cattle ear tags (active ingredient = Cyano [3-phenoxyphenyl] methyl-4-chloro-alpha-[1-methylethyl] benzenecetate) in the cups to kill the trapped insects. Results of a preliminary study using eartags placed in traps indicated they had no effect on ground beetle catch (French 1998). For each trap, we buried a piece (≈ 30 cm long) of PVC plastic pipe (13 cm i.d.) in the soil so that the top of the pipe was ≈ 2 cm below the soil surface, which allowed setting the lips of the funnels at the soil surface. The

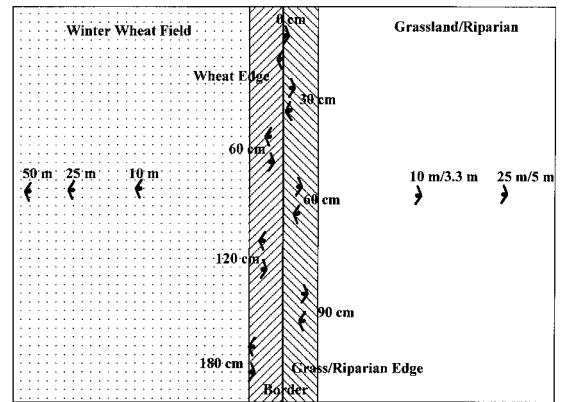


Fig. 1. Arrangement of directional pitfall traps in wheat fields, grasslands, riparian zones, and their edges. Traps were placed at varying distances from the border. The border represented an abrupt change in vegetation from wheat to natural vegetation.

PVC pipes supported the traps and prevented soil from collapsing around them. To increase the capture efficiency of the traps, we used galvanized sheet metal strips (14 by 122 cm) as guides (Durkis and Reeves 1982). The guides were angled forward slightly and driven into the soil a few centimeters. We positioned the traps at the centers of the guides to catch beetles walking in a particular direction.

Approximately 2 wk before planting of wheat, we placed six traps in each of the two wheat fields on 21 September and sampled weekly through 5 October. These traps were set to ascertain the ground beetle fauna in the fallow wheat fields. We placed two traps in the fallow fields 50 m from the grassland border and two traps 50 m from the riparian border. These traps were separated by ≈ 400 m. We also set two additional traps near the center of the fallow fields ≈ 200 m from the edges. These six traps were removed after the last sample date. To determine the ground beetle fauna in the natural habitats before wheat emergence, we established 10 traps in the grasslands, riparian zones, and their edges (see below) on one October and sampled weekly through 15 October. Wheat was planted on 10 October at site 1 and on 14 October at site 2. For each site, all 19 traps were set on 15 October and checked weekly through 9 June 1997, shortly before wheat harvest (237 d). Note that traps could not be checked on 13 January due to adverse weather conditions and only 33 sampling dates were collected. The arrangement of the pitfall trap network in grasslands, riparian zones, winter wheat fields, and their boundaries is illustrated in Fig. 1. We placed traps in the wheat fields at 10, 25, and 50 m from the border. At the wheat field edges, we set pairs of traps at 60, 120, and 180 cm from the border. The 10 traps cited above were established as follows. At the grassland and riparian edges, we set pairs of traps at 30, 60, and 90 cm from the border. We also placed paired traps exactly on the border (0 cm). We used different distances in the edges in an attempt to determine how far different species of beetles

would disperse into the wheat fields (French 1998). The paired traps were set facing opposite directions to allow us to estimate net dispersal of the ground beetles across the boundaries. In the riparian zones we placed traps at 3 and 5.5 m from the border, whereas, in the grasslands we set traps at 10 and 25 m from the border. Seventy-six directional pitfall traps were used in this study representing 18,012 trapping days.

Numbers generated from pitfall trap catches alone do not provide estimates of absolute density, rather activity density, which is a function of a species population size, activity, and ease of capture (Greenstade 1964). Sampling continuously over a period of weeks or months with pitfall traps effectively estimates relative abundance of species within a habitat and permits comparison of abundance among years or seasons in that habitat (Baars 1979). However, one must be cautious about interpreting differences in relative abundances among habitats, as species differ in catchability depending on trap type and habitat (Luff 1975, Halsall and Wratten 1988, Morrill et al. 1990, Spence and Niemelä 1994).

Data Analysis. We used the computer program CANOCO (ter Braak 1987) to perform canonical correspondence analysis on species abundance data. Canonical correspondence analysis relates species abundances to environmental variables and is a robust method for analyzing data from pitfall traps (Palmer 1993). We included the following 15 environmental indicator variables, autumn, winter, spring, site 1g, site 2g, site 1r, site 2r, grassland, grassland edge, grassland-wheat edge, grassland-wheat interior, riparian zone, riparian edge, riparian-wheat edge, and riparian-wheat interior in canonical correspondence analyses. We used a partial canonical correspondence analysis to focus on the effects of the eight habitats on species abundances by using seasons and sites as covariables and removing their effects before conducting canonical correspondence analysis. To relate species assemblages among habitats, only beetles captured on more than five occasions were used in the canonical correspondence analyses. Abundance data were transformed to square roots before canonical correspondence analysis. We used Monte Carlo permutation tests to determine the significance of community patterns (ter Braak 1987). We used 199 permutations in all analyses.

The paired traps located in the habitat edges were intended to provide information on net displacement at the various trap distances. Thus, we used paired *t*-tests to assess differences in direction and location in the number of beetles captured in the edge traps. In addition, we compared the number of beetles captured in each particular habitat (i.e., natural interiors, natural edges, wheat edges, and wheat interiors) with respect to season of capture (i.e., autumn, winter, and spring). These data were analyzed with contingency chi-square tests. For autumn and winter analyses, beetle catches were recoded to 'zero' for no beetles captured and 'not zero' for one or more beetles captured. We employed only these two categories because of the low number of beetles captured during these time

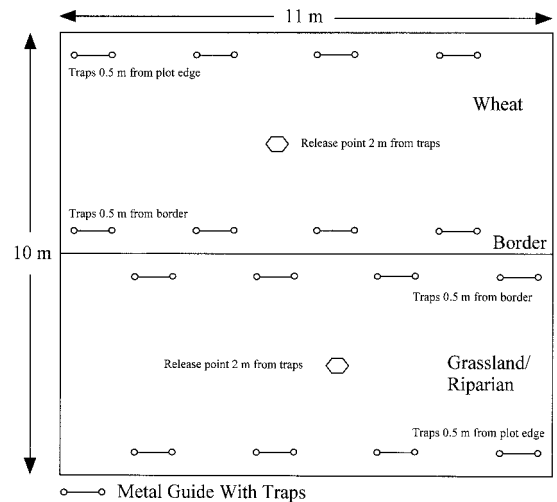


Fig. 2. Arrangement of guided pitfall traps in the mark-recapture study. The border represented an abrupt change in vegetation from wheat to natural vegetation.

periods. Because most beetles were captured during spring, we used three categories: 'zero' for no beetles captured, 'small' for 1–4 beetles captured, and 'large' for five or more beetles captured.

Mark-Recapture. We used a mark-recapture method to verify ground beetle dispersal across boundaries. A 10 by 11-m plot was established at site 1 at the grassland-wheat field boundary on 21 March 1997 (Fig. 2). We established eight pairs of pitfall traps, with each pair connected by a metal guide, in each subplot to capture ground beetles. We placed four traps 0.5 m from the grassland-wheat field border and four traps 0.5 m from the edge of each subplot in each habitat. The borders represented the disturbance lines separating the cultivated wheat fields from the natural habitats. Trap design followed that of Morrill (1975). These traps consisted of a 455-ml Solo cup (Concept Communications, Burr Ridge, IL) with a 145 mm i.d., a Solo Cozy Cup funnel, and an inner 148 ml Solo cup. We placed a cover over the cups to protect captured beetles from direct sunlight. Galvanized sheet metal strips (14 by 122 cm) were used to increase the capture of beetles by channeling their movement into the traps. We marked captured beetles with Testors (Testor, Rockford, IL) enamel paint on the pronotum and elytra (Southwood 1978). Preliminary marking on *Pasimachus elongatus* LeConte, a species with a smooth exoskeleton and inclination to burrow, maintained in the laboratory indicated the mark was durable over several weeks to several months. We applied a different mark each day of the study to the pronotum, upper left elytra, lower left elytra, upper right elytra, or lower right elytra of beetles captured that day. To distinguish beetles captured in grassland from those captured in wheat fields and to determine which beetles crossed the borders, we used two sets of five different colors. One set of paint was used for beetles captured in the grassland and the

Table 1. List of species captured in the primary study and in the mark-recapture study

Species	No.	Abbr.	Mark-Recapture		Primary study	
			G-W	R-W	G-W	R-W
<i>Abacids permundus</i> Say	101	Abp	Both	—	Both	Both
<i>Acupalpus testaceus</i> Dejean	1		—	—	—	Riparian
<i>Agonum decorum</i> Say	4		—	—	—	Both
<i>A. nutans</i> Say	4		Wheat	—	Grass	Both
<i>A. octopunctatum</i> F.	1		—	—	Grass	—
<i>A. pallipes</i> F.	68	Agp	—	—	Both	Both
<i>A. punctiforme</i> Say	201	Apu	Both	Wheat	Both	Both
<i>Amara convexa</i> LeConte	32	Amc	↔	→	Both	Both
<i>A. cupreolata</i> Putzeys	63	Acu	→	—	Both	Both
<i>A. impuncticollis</i> Say	1		—	Riparian	—	Riparian
<i>A. musculus</i> Say	14	Amm	Both	—	Both	Both
<i>A. obesa</i> Say	4		Wheat	—	Wheat	Both
<i>A. pennsylvanica</i> Hayward	2		Both	Both	Both	—
<i>A. rubrica</i> Haldeman	17	Amr	Grass	—	Both	Both
<i>Amphasia interstitialis</i> Say	1		—	—	—	Riparian
<i>Anisodactylus carbonarius</i> Say	45	Anc	↔	↔	Both	Both
<i>A. dulcicollis</i> LaFerté	1,140	And	→	→	Both	Both
<i>A. harpaloides</i> LaFerté	26	Anh	→	Both	Both	Both
<i>A. merula</i> Germar	214	Anm	↔	↔	Both	Both
<i>A. opaculus</i> LeConte	0		Both	Both	—	—
<i>A. ovularis</i> Casey	27	Ano	↔	↔	Both	Both
<i>A. rusticus</i> Say	344	Anr	Both	Both	Both	Both
<i>A. sanctaecrucis</i> F.	16	Ans	Wheat	Riparian	Both	Both
<i>A. verticalis</i> Say	4		—	—	—	Riparian
<i>Apenes sinuata</i> Say	5		—	Riparian	—	Riparian
<i>Apristus latens</i> LeConte	16	Apl	Both	Both	Both	Both
<i>Atraneus pubescens</i> Dejean	3		Grass	—	—	Both
<i>Badister notatus</i> Hayward	1		—	Riparian	Grass	—
<i>Bembidion castor</i> Lindroth	943	Bec	Both	↔	Both	Both
<i>B. nigripes</i> Kirby	2,074	Ben	Both	↔	Both	Both
<i>B. texanum</i> Chaudoir	1		—	—	—	Riparian
<i>Calathus opaculus</i> LeConte	188	Cao	→	Riparian	Both	Both
<i>Calosoma affine</i> Chaudoir	162	Caf	↔	←	Both	Both
<i>C. externum</i> Say	104	Cae	→	Both	Both	Both
<i>C. sayi</i> Dejean	1		—	—	—	Riparian
<i>C. scrutator</i> F.	6	Cas	Grass	—	—	Both
<i>C. wilcoxi</i> LeConte	4		—	—	—	Both
<i>Catogenus rufus</i> F.	1		—	—	—	Riparian
<i>Chlaenius emarginatus</i> Say	1		—	—	—	Wheat
<i>C. nemoralis</i> Say	1		—	—	—	Wheat
<i>C. pennsylvanicus</i> Say	1		—	—	—	Wheat
<i>C. platyderus</i> Chaudoir	19	Cpl	—	Wheat	Grass	Both
<i>C. sericeus</i> Forst	1		—	—	Wheat	—
<i>C. tomentosus</i> Say	69	Cht	→	→	Both	Both
<i>Cicindela denverensis</i> Casey	11	Cid	—	Wheat	Wheat	Both
<i>C. punctulata</i> Olivier	51	Cip	—	—	Both	Both
<i>C. scutellaris</i> Say	1		—	—	Wheat	—
<i>Clivina bipustulata</i> F.	201	Clb	Both	←	Both	Both
<i>C. postica</i> LeConte	92	Clp	Both	Both	Both	Both
<i>Colliuris pennsylvanica</i> L.	121	Cop	Both	Wheat	Both	Both
<i>Crataeanthus dubius</i> Beauvois	73	Crd	Both	Both	Both	Both
<i>Cyclotrachelus constrictus</i> Say	3		Grass	—	Grass	Riparian
<i>C. seximpressus</i> LeConte	0		Both	—	—	—
<i>C. torvus</i> LeConte	88	Cyt	↔	—	Both	Both
<i>Cymindis laticollis</i> Say	8	Cyl	—	—	Both	Riparian
<i>C. pilosa</i> Say	11	Cyp	—	—	Both	Riparian
<i>Dicaelus elongatus</i> Bonelli	14	Die	—	Both	Grass	Both
<i>Discoderus parallelus</i> Halderman	56	Dip	Wheat	—	Both	Both
<i>Dyschiriodes globulosus</i> Say	66	Dyg	Wheat	Both	Both	Both
<i>D. pilosus</i> Say	20	Dyp	Wheat	Both	Grass	Both
<i>Elaphropus dolosus</i> LeConte	65	Eld	Both	Wheat	Both	Both
<i>E. granarius</i> Dejean	56	Elg	Both	Wheat	Both	Both
<i>Euryderus grossus</i> Say	0		—	Wheat	—	—
<i>Galerita atripes</i> LeConte	22	Gaa	—	Both	Wheat	Both
<i>G. janus</i> F.	201	Gaj	Both	↔	Both	Both
<i>Harpalus amputatus</i> Say	15	Haa	Wheat	—	Both	Both
<i>H. caliginosus</i> F.	2		—	—	Wheat	Riparian
<i>H. desertus</i> LeConte	34	Had	—	→	Both	Both
<i>H. faunus</i> LeConte	52	Haf	—	Riparian	Both	Riparian
<i>H. fulgens</i> Csiki	198	Hfu	→	Both	Both	Both
<i>H. paratus</i> Say	6	Hap	—	Riparian	—	Riparian

Table 1. Continued.

Species	No.	Abbr.	Mark-Recapture		Primary study	
			G-W	R-W	G-W	R-W
<i>H. pensylvanicus</i> DeGeer	512	Hpe	—	—	Both	Both
<i>Hellomorphoides praeustus</i> Harris	36	Hep	—	↔	—	Both
<i>Lebia analis</i> Dejean	2		—	—	—	Riparian
<i>L. atriventris</i> Say	5		Wheat	—	—	Both
<i>L. solea</i> Hentz	4		—	—	Grass	Both
<i>L. tricolor</i> Say	13	Let	—	Riparian	—	Both
<i>L. viridis</i> Say	1		—	—	Wheat	—
<i>Microlestes linearis</i> LeConte	11	Mil	—	—	Both	Both
<i>Notiobia terminata</i> Say	3		Wheat	Riparian	Wheat	Both
<i>Notiophilus novemstriatus</i> LeConte	252	Non	—	Both	Both	Both
<i>Olisthopus parvatus</i> Say	4		Both	Both	Wheat	Riparian
<i>Omophron americanum</i> Dejean	3		—	—	Wheat	Wheat
<i>Panagaeus fasciatus</i> Say	3		Both	Both	—	Both
<i>Pasimachus elongatus</i> LeConte	31	Pae	↔	Both	Both	Both
<i>Pterostichus chalcites</i> Say	345	Ptc	Both	Both	Both	Both
<i>P. femoralis</i> Kirby	23	Ptf	Both	—	Both	Both
<i>P. lucublandus</i> Say	3		—	—	—	Riparian
<i>Scaphinotus cavicollis</i> Say	3		—	—	Both	Wheat
<i>Scarites subterraneus</i> F.	168	Scs	↔	Both	Both	Both
<i>Selenophorus opalinus</i> LeConte	1		—	—	—	Riparian
<i>S. planipennis</i> LeConte	0		—	Both	—	—
<i>Stenolophus comma</i> F.	30	Stc	—	Riparian	Both	Both
<i>S. conjunctus</i> Say	248	Sco	Both	Both	Both	Both
<i>S. lineola</i> F.	9	Stl	—	Wheat	Both	Wheat
<i>S. ochropepus</i> LeConte	16	Sto	—	—	Wheat	Both
<i>S. rotundatus</i> LeConte	26	Str	—	—	Both	Both
<i>Stenomorphus californicus</i> LeConte	1		—	—	Grass	—

Also presented is the number of beetles captured for each species in the primary study, and abbreviations (Abbr.) of species depicted in canonical correspondence analysis and partial canonical correspondence analysis biplots. For the mark-recapture study, the arrows indicate the direction that ground beetles crossed the borders (G-W, grassland-wheat field boundary; R-W, riparian zone-wheat field boundary). Also listed are species that were captured in only one habitat (grass, riparian, or wheat), in both grasslands and wheat fields (Both), or in both riparian zones and wheat fields (Both). Many of these species were captured in low numbers and we could not verify movement across the borders. —, Species not captured in the primary study or in the mark-recapture study. Because of their small size, we treated *Bembidion nigripes* and *B. castor* as *Bembidion* spp., *Elaphropus dolosus* and *E. granaries* as *Elaphropus* spp., and *Dyschiroides globulosus* and *D. pilosus* as *Dyschiroides* spp. in the mark-recapture study. *Anisodactylus opaculus*, *Cyclotrachelus seximpressus*, *Euryderus grossus*, and *Selenophorus planipennis* were captured only in the mark-recapture study.

other set for beetles captured in wheat. This allowed 25 d of marking before reusing a specific color at a specific location on a beetle. Beetles were captured, returned to the laboratory, processed, held overnight, and then released into the center of the subplot in which they were captured (Fig. 2). An identical plot was established on the riparian zone-wheat field boundary at site 1 on 22 April 1997. We assumed that beetles collected and marked in the riparian/wheat plot would not be captured in the grassland/wheat plot (and vice versa). We checked all traps daily through 4 June 1997.

Results

Temporal Distribution of Ground Beetle Assemblages. We captured 9,151 ground beetles representing 94 species (Table 1). We observed two peaks in activity; a small peak occurred in autumn followed by a decrease in activity during winter, and then a second, large peak in spring (Fig. 3). This pattern was similar in the grassland-wheat field and riparian zone-wheat field sites.

The eigenvalues of the canonical correspondence analysis measure the proportion of total variation in ground beetle abundance explained by their respec-

tive axis (ter Braak 1986, 1987, 1995). The eigenvalues for canonical correspondence analysis axes 1 through 4 were 0.455, 0.235, 0.171, and 0.107. Axis 1 explained 38.3% of the species–environment relationship, and together with axis 2, explained 58.1% of the species–

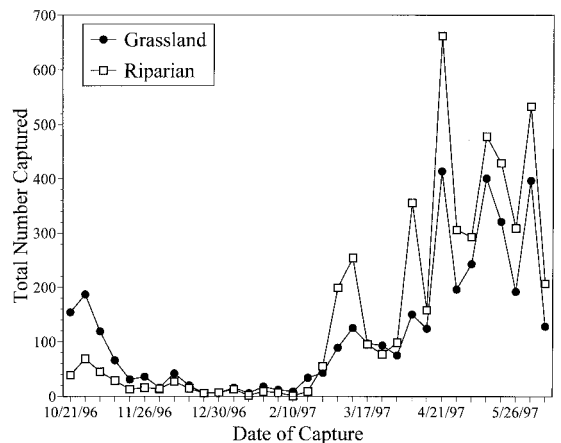


Fig. 3. Total number of ground beetles captured by date from the grassland-wheat field and riparian-wheat field sites.

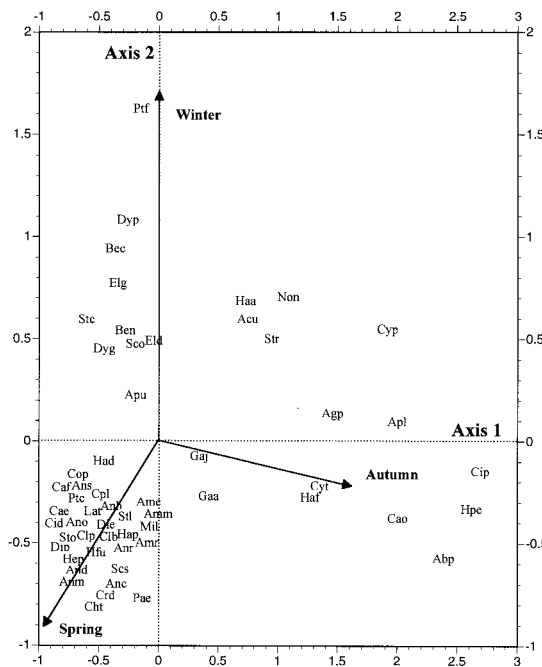


Fig. 4. Biplot of ground beetle abundances and seasonal variables from canonical correspondence analysis. The abbreviations of species names are plotted and complete names are listed in Table 1. Environmental variables; autumn, winter, and spring are represented by arrows.

environment relationship. Combined, axes 1 through 4 explained 81.5% of the total species–environment relationship. A biplot of the environmental variables and species scores (sites not shown) illustrates that axes 1 and 2 represent seasonal gradients (Fig. 4). Species names and abbreviations are given in Table 1. Arrows represent environmental variables, and a long arrow positioned close to an axis indicates a strong relationship with that axis (ter Braak 1986, Palmer 1993), such as autumn and axis 1 (Fig. 4). Ground beetles positioned close to the arrows have a strong association with that variable, for example the abundance of *Cyclotrachelus torvus* (Cyt) is strongly associated with autumn (Fig. 4). Autumn dominating beetles ordinated to the right of axis 2 and near axis 1. In contrast, beetles that predominated in spring ordinated to the left of axis 2 and below axis 1. Beetles that were abundant in winter ordinated above axis 1 and near axis 2. The observed associations of ground beetles with environmental variables differed significantly from random (Monte Carlo test statistic = 7.38, $P < 0.01$).

Spatial Distribution of Ground Beetle Assemblages.

A partial canonical correspondence analysis determined the effects of habitats on patterns of species abundance. In the partial canonical correspondence analysis, effects of seasons and sites on species composition were factored out as covariables. The eigenvalues for axes 1 through 4 were 0.121, 0.053, 0.035, and 0.020. Again, these values measure the amount of vari-

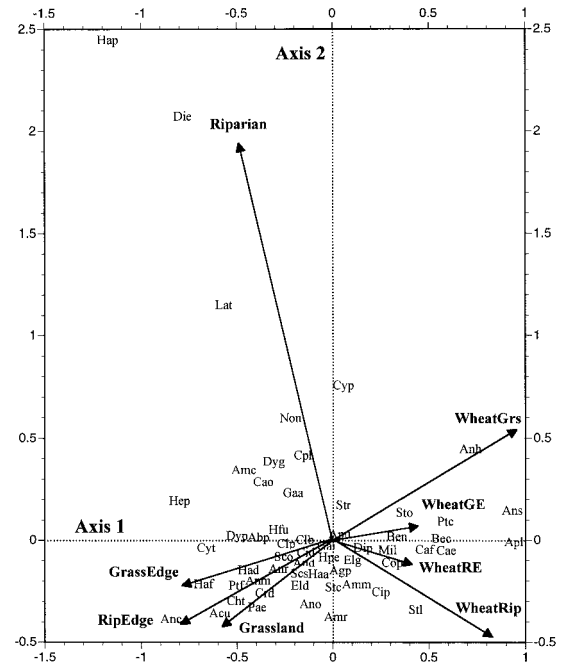


Fig. 5. Biplot of ground beetle abundances and environmental variables from a partial canonical correspondence analysis. The abbreviations of species names are plotted and complete names are listed in Table 1. Arrows represent environmental variables. The environmental variables are riparian interior = Riparian, riparian edge = RipEdge, wheat interior adjacent to riparian zones = WheatRip, wheat edge adjacent to riparian zones = WheatRE, grassland interior = Grassland, grassland edge = GrassEdge, wheat interior adjacent to grassland = WheatGr, wheat edge adjacent to grassland = WheatGE.

ation in species scores explained by their respective axis, with axis 1 explaining more variation in species scores than axes 2, 3, and 4. Axis 1 explained 47.6% of the species–environment relationship remaining after factoring out the covariables, and together with axes 2–4, explained 90.0% of the species–environment relationship. Axis 1 separated wheat field assemblages from natural habitat assemblages (Fig. 5). Assemblages associated with wheat fields ordinated to the right of axis 2, whereas assemblages associated with natural habitats ordinated to the left of axis 2. Beetle assemblages were further separated along axis 2. Species associated with riparian interiors ordinated above axis 1. In contrast, beetle assemblages were very similar in riparian zone edges, grassland edges, and grassland interiors, where they ordinated to the left of axis 2 and below axis 1. The ordering of beetle species in wheat interiors and wheat edges adjacent to grasslands occurred in the positive space of axes 1 and 2. In contrast, the ordering of beetle species in wheat interiors and wheat edges adjacent to riparian zones occurred in the positive space of axis 1 and the negative space of axis 2. There was a clear distinction between assemblages in wheat interiors adjacent to grasslands from assemblages in wheat interiors adja-

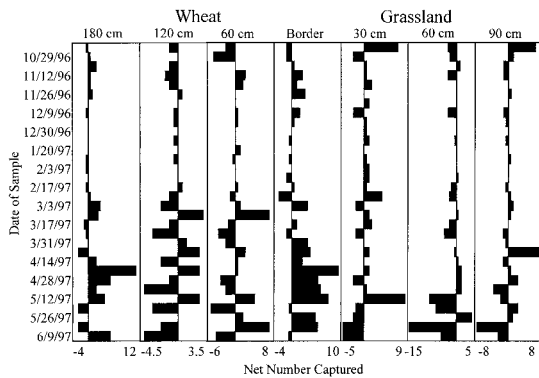


Fig. 6. Net dispersal of ground beetles from traps positioned in the grassland edge and wheat field edge. Directions of bars indicate net direction of dispersal.

cent to riparian zones (Fig. 5). This pattern was significantly different from random (Monte Carlo test statistic = 2.91, $P < 0.01$), indicating that it reflected a meaningful ecological pattern.

Ground Beetle Dynamics at Boundaries. It is presumed that natural enemies of agricultural pests cannot survive the tillage and other treatments applied to most agricultural lands and that they disperse into agricultural fields from surrounding natural or nonarable habitats (Wissinger 1997). Furthermore, several studies from temperate regions have shown that ground beetles move from field interiors into field boundaries to overwinter and back into fields in spring (Wallin 1985, Coombes and Sotherton 1986, Duelli et al. 1990, Wratten and Thomas 1990). The canonical correspondence analysis results indicated three distinct ground beetle assemblages occurring in autumn, winter, and spring. If the patterns of movement described above occur in Oklahoma, we should capture more beetles moving out of the grassland and riparian habitats and into the wheat fields during early autumn as the wheat emerges. As winter approaches, we expect dispersal of beetles back into the riparian and grassland habitats. As with the northern latitudes, we then expect to capture more beetles moving out of the grassland and riparian habitats and into the wheat fields during spring.

The differences in paired boundary traps are in Figs. 6 and 7. We performed paired t -tests on the paired traps to determine differences in direction of number of beetles captured. At the grassland-wheat field sites, we found significant differences at 60 cm into the grass ($t = -2.57$, $df = 32$, $P < 0.05$), at the border ($t = 3.56$, $df = 32$, $P < 0.01$), and at 120 cm into the wheat field ($t = 2.25$, $df = 32$, $P < 0.05$). At the riparian-wheat field sites, we found a significant difference only at 60 cm into the wheat field ($t = -3.18$, $df = 32$, $P < 0.01$). These paired t -tests however, do not test for patterns of movement; they only indicate overall differences in numbers captured. The patterns of dispersal for all ground beetles are determined here by visual inspection (Figs. 6 and 7). During the first week of trapping in autumn, immediately after planting, there was a net

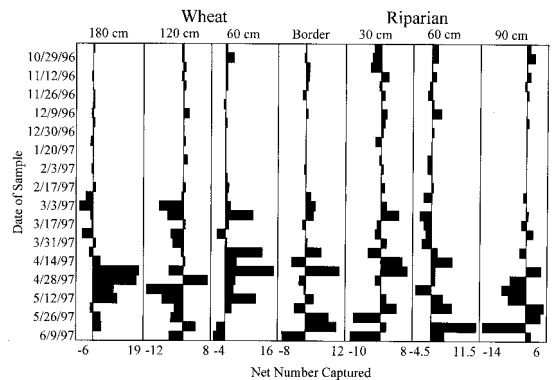


Fig. 7. Net dispersal of ground beetles from traps positioned in the riparian edge and wheat field edge. Directions of bars indicate net direction of dispersal.

increase in the number of beetles captured from the border to 180 cm into the wheat field at the grassland-wheat field boundary, but not at the riparian-wheat field boundary (Figs. 6 and 7). During the second week, this trend extended only 60 cm into the wheat field from the grassland. No clear trend in net movement into the wheat field from the grassland edge was observed following the second week. However, in late autumn there was a perceptible trend of movement into the area between 30 and 60 cm into the grassland edge, whereas in the riparian-wheat field boundary dispersal seemed to continue beyond 90 cm into the riparian edge. During winter, the number of beetles captured was low and net dispersal into natural habitats was not detectable. Except for beetles captured at the grassland-wheat field border, net movement from the natural habitats into the wheat fields was not obvious during late winter and early spring. No trend in net displacement was observed as the population of ground beetles increased during spring.

Although seasonal trends in ground beetle dispersal into wheat fields from natural habitats were difficult to detect, we verified using mark-recapture studies that several species routinely crossed boundaries by walking (Table 1). Of the 94 species captured, 67 were collected in the mark-recapture study. These 67 species represented 71% of all ground beetles captured and 80% of beetles captured in spring. We determined that 45 of these 67 species of ground beetles captured had moved across the borders or were captured in both the natural habitats (grassland or riparian) and the adjacent wheat fields (Table 1). Most other species were captured only a few times.

The dispersal of these beetles apparently resulted in differences in numbers captured with respect to trap location and sampling date. Based on traps facing the border, which allowed direct comparisons of edge traps with interior traps, we captured significantly more beetles in grassland edges and significantly fewer beetles in wheat interiors during autumn than in the other habitats ($\chi^2 = 13.02$, $df = 3$, $P < 0.01$; Fig. 8). This pattern continued through winter ($\chi^2 = 9.37$, $df = 3$, $P < 0.05$). However, a significant shift in

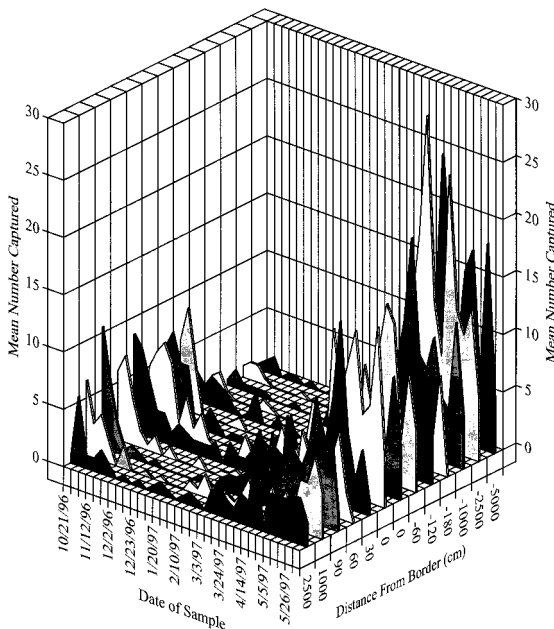


Fig. 8. Mean number of ground beetles captured by habitat and sampling date for grassland-wheat field locations. Data are from traps facing the border.

capture rates among habitats occurred in late winter through spring, with more beetles being captured in wheat field interiors than in the other habitats ($\chi^2 = 29.09$, $df = 6$, $P < 0.001$).

The pattern of beetles captured also varied over seasons in the riparian zones and wheat fields. We captured significantly more beetles in riparian and wheat edges than in the other habitats during autumn ($\chi^2 = 27.89$, $df = 3$, $P < 0.001$; Fig. 9). During winter, there was no significant difference in the number of beetles captured among habitats. However, as with the grassland-wheat field situation, a significant shift in capture rates among habitats occurred in late winter through spring, with more beetles being captured in wheat field interiors than in the other habitats ($\chi^2 = 32.71$, $df = 6$, $P < 0.001$). These shifts in capture rates coincided with the overall increase in numbers captured during late winter and spring, indicating dispersal into wheat field interiors (Fig. 3). Lending further support to our contention that beetles crossed the boundaries from natural habitats to colonize wheat fields is the observation that we captured only 14 species in the fallow wheat field just before planting, and most of these were caught in very low numbers, while we captured 22 and 24 species in much higher numbers in the grasslands and riparian zones during the same time interval (Table 2).

Discussion

Season had a profound effect on the structure of ground beetle assemblages. Species composition in autumn, winter, and spring represented unique assem-

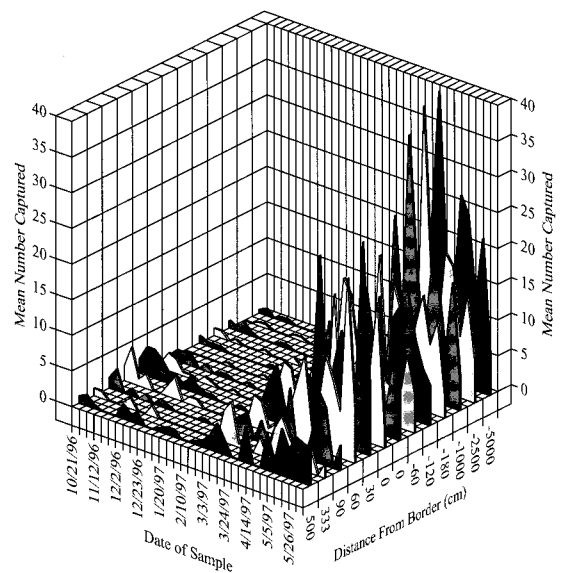


Fig. 9. Mean number of ground beetles captured by habitat and sampling date for riparian-wheat field locations. Data are from traps facing the border.

blages of ground beetles. The spring and autumn assemblages correspond to the peaks in activity observed in our study. The spring peak was much greater than the autumn peak. Activity of ground beetles in autumn and spring is related to their life cycles, where species active in the spring generally overwinter as adults, and species active in autumn generally overwinter as larvae (Allen 1979, Luff 1987). Activity of most insects is driven by temperature (Southwood 1978). Thus, the spring peak we observed might be related to the time when temperatures are increasing, and autumn peak may be related to the time when temperatures are decreasing. In a study conducted at a similar latitude to our study, Allen and Thompson (1977) found spring and autumn peaks for many species of ground beetles in hardwood and pine forests in northwestern Arkansas. In their study, spring peaks in activity were also much greater than autumn peaks. At these lower latitudes, some species may not be restricted to a single period of activity, and these species may be bivoltine or multivoltine under favorable conditions (Luff 1987). Bivoltine or multivoltine species may comprise the winter ground beetle assemblage in our study.

Landscape patches interact through their boundaries (Wiens et al. 1985). A boundary consists of an edge from each adjacent patch and a border separating the edges (Duelli et al. 1990, Forman and Godron 1986). Boundaries are characterized by steep ecological gradients in factors such as temperature, relative humidity, wind speed, and vegetation structure. Organisms may respond to these gradients differently, such that the boundary selectively filters organisms as they disperse across it. This filtering process influences the species composition in boundaries and the habitats they separate. Duelli et al. (1990) noted differences in

Table 2. Total number of ground beetles captured by species in fallow fields prior to planting of wheat, and in grasslands and riparian zones while wheat was being planted

Species	21/9–10/5	1/10–15/10	1/10–15/10
	Fallow	Grassland	Riparian
<i>Abacidus permundus</i>	0	31	9
<i>Agonum pallipes</i>	0	2	3
<i>Amara impuncticollis</i>	0	0	1
<i>Amara rubrica</i>	1	2	1
<i>Anisodactylus rusticus</i>	2	7	6
<i>A. harpaloides</i>	1	0	1
<i>A. dulcicollis</i>	0	1	0
<i>Apenes sinuata</i>	0	0	1
<i>Apristus latens</i>	2	2	9
<i>Bembidion nigripes</i>	0	1	0
<i>Calathus opaculus</i>	0	14	10
<i>Calosoma affine</i>	0	0	1
<i>Chalenius tomentosus</i>	1	2	1
<i>Cicindela punctulata</i>	14	20	22
<i>Clivina bipustulata</i>	0	2	3
<i>C. postica</i>	0	1	0
<i>Cratacanthus dubius</i>	2	1	0
<i>Cyclotrachelus torvus</i>	1	7	13
<i>Elaphropus dolosus</i>	0	1	1
<i>Galerita atripes</i>	0	0	3
<i>Galerita janus</i>	0	2	24
<i>Harpalus caliginosus</i>	1	0	0
<i>H. faunus</i>	3	15	11
<i>H. fulgens</i>	0	1	0
<i>H. pensylvanicus</i>	15	123	96
<i>Notiophilus novemstriatus</i>	0	0	12
<i>Pasimachus elongatus</i>	2	0	1
<i>Pterostichus chalcites</i>	1	2	5
<i>Scarites subterraneus</i>	11	2	1
<i>Stenolophus rotundatus</i>	0	0	1
<i>Stenomorphus californicus</i>	0	1	0
Grand total	57	239	236

ground beetle species dispersing across boundaries in a mosaic of cultivated and natural habitats, and this resulted in different species assemblages among the habitats. We also found differences in beetle assemblages in the habitats we studied. Grassland, grassland edge, and riparian edge assemblages were similar and shared most species. However, the riparian interior assemblage was unique sharing very few species with the other habitats. We found two distinct assemblages of ground beetles in wheat fields. One was the assemblage adjacent to grasslands and the other was the assemblage adjacent to riparian zones.

The differences in wheat field interior assemblages may have resulted from the dispersal of ground beetles from the natural habitats. The boundaries apparently filtered species of ground beetles as they dispersed from grasslands and riparian zones into adjacent wheat fields. Although not conclusive from our measurements of net dispersal of beetles, the mark-recapture studies showed that several species readily crossed the boundaries from grasslands and riparian zones into wheat fields. Therefore, it seems reasonable that, because ground beetles generally disperse by walking, the additional species observed in the wheat fields originated from the adjacent grassland and riparian habitats. This notion is also supported by the differences in the distributions of beetles captured by habitat.

Wissinger (1997) suggested that the most effective natural enemies of annual crop pests are "cyclic col-

onizers" of the ephemeral crop system. He described cyclic colonizers as insects that respond to disturbance by dispersing to permanent habitats, delay reproduction, overwinter, and then recolonize the crop the following year. Before fragmenting the landscape for agricultural purposes, cyclic colonizers would probably be species or subpopulations of species that inhabited natural boundaries between riparian zones and grasslands or between forests and grasslands. It is at these boundaries where disturbance and the flux of materials and organisms are greatest (Wiens et al. 1985, Wiens 1997). Wissinger (1997) suggested that insects occupying these boundaries are preadapted for survival and reproduction in agricultural landscapes. In other words, these insects had already evolved life history traits that allow them to exploit changing, but predictable environments, and possess enough additive genetic variation underlying these traits to evolve in response to additional human disturbances to the landscape.

In reference to ground beetles, habitat generalists may have been the beneficiaries of modern agriculture. Modern agriculture provides a mosaic of arable and nonarable habitats for ground beetles. From this study, several species are potential biological control agents of wheat pests. Because wheat fields vary considerably in size in the Great Plains, it is important to determine whether ground beetles overwinter in adjacent grassland and riparian edges, and if they do, how far they will disperse into the wheat field interior. Equally important is to determine which species have life cycles that are completed exclusively in crop fields. For such species, survival and reproduction depends entirely on availability of prey in the wheat fields.

Ground beetle assemblages differed with respect to seasons and habitats. We could not clearly demonstrate net dispersal of ground beetles from grassland and riparian habitats into wheat fields. This may be due, in part, to the weekly sampling period. One week may be too long to measure net dispersal. That is, given the high abundance and mobility of ground beetles, it may be necessary to measure net dispersal on a daily basis. A shorter sampling period, such as a day, may clearly reveal the predicted patterns of seasonal dispersal. Regardless, based on all data presented here, many species dispersed from the grassland and riparian habitats into the wheat fields and that their dispersal resulted in different structure of wheat field interior assemblages adjacent to different habitats. Because of their continuous seasonal activity and predatory nature, ground beetles are good candidates for biological control of wheat pests.

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product does not constitute an endorsement or a recommendation by the USDA for its use.

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